

University of Groningen

Differences in speed and duration of bird migration between spring and autumn

Nilsson, Cecilia; Klaassen, Raymond H. G.; Alerstam, Thomas

Published in:
American Naturalist

DOI:
[10.1086/670335](https://doi.org/10.1086/670335)

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version
Publisher's PDF, also known as Version of record

Publication date:
2013

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

Nilsson, C., Klaassen, R. H. G., & Alerstam, T. (2013). Differences in speed and duration of bird migration between spring and autumn. *American Naturalist*, 181(6), 837-845. <https://doi.org/10.1086/670335>

Copyright

Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

The publication may also be distributed here under the terms of Article 25fa of the Dutch Copyright Act, indicated by the "Taverne" license. More information can be found on the University of Groningen website: <https://www.rug.nl/library/open-access/self-archiving-pure/taverne-amendment>.

Take-down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Downloaded from the University of Groningen/UMCG research database (Pure): <http://www.rug.nl/research/portal>. For technical reasons the number of authors shown on this cover page is limited to 10 maximum.

Differences in Speed and Duration of Bird Migration between Spring and Autumn

Cecilia Nilsson,^{1,*} Raymond H. G. Klaassen,^{1,2} and Thomas Alerstam¹

1. Department of Biology, Lund University, Sweden; 2. Dutch Montagu's Harrier Foundation and Animal Ecology Group, University of Groningen, The Netherlands

Submitted August 21, 2012; Accepted February 19, 2013; Electronically published April 24, 2013

Dryad data: <http://dx.doi.org/10.5061/dryad.82d4q>.

ABSTRACT: It has been suggested that birds migrate faster in spring than in autumn because of competition for arrival order at breeding grounds and environmental factors such as increased daylight. Investigating spring and autumn migration performances is important for understanding ecological and evolutionary constraints in the timing and speed of migration. We compiled measurements from tracking studies and found a consistent predominance of cases showing higher speeds and shorter durations during spring compared to autumn, in terms of flight speeds (airspeed, ground speed, daily travel speed), stopover duration, and total speed and duration of migration. Seasonal differences in flight speeds were generally smaller than those in stopover durations and total speed/duration of migration, indicating that rates of foraging and fuel deposition were more important than flight speed in accounting for differences in overall migration performance. Still, the seasonal differences in flight speeds provide important support for time selection in spring migration.

Keywords: bird migration speed, duration of migration, flight speed, stopover, optimal migration, timing of migration.

Introduction

It has often been suggested that prebreeding (spring) migration may be more time constrained than postbreeding (autumn) migration because of strong competition for spring arrival order among individuals of a population where prior residency gives advantages in the competition for the best breeding territories (Kokko 1999). Birds that arrive early start breeding earlier (Moore et al. 2005), which can increase reproductive performance (van Noordwijk et al. 1995). They will also have more time to breed and raise fledged young that are ready to migrate at the end of the summer (McNamara et al. 1998). Selection for early arrival date will shift arrival dates to earlier in the season and away from the optimal arrival date based on

resource availability (Kokko 1999). Departure time from the wintering grounds is likely to be affected by a trade-off between resources available at the wintering grounds and resources available along the migration route and on the breeding grounds at the time of arrival. If birds are forced by competition to migrate when resources at the breeding grounds are still scarce, there could be selection for remaining at the wintering grounds as long as possible and increasing migration speed to still arrive as early as possible at the breeding grounds.

There are only a few studies based on ringing and capture data that have specifically investigated the possible difference between spring and autumn migration speeds among birds, and these indicated a faster spring migration compared to autumn migration among songbirds in the European-African migration systems (Fransson 1995; Yohannes et al. 2009). But knowledge of bird migration routes and timing of migration is increasing rapidly with the use of new technology for tracking individual birds (Robinson et al. 2010; Bridge et al. 2011). Therefore, we can now examine recent tracking studies in order to compare speeds and durations of spring and autumn migrations and discuss the key components of migration speed. We base this discussion on detailed studies of the same individual birds (satellite tracking, geolocator studies) and, in some cases, the same populations of birds (radar tracking, capture data) on both spring and autumn migrations. Birds are the most studied of the migrating taxa, but our approach and reasoning will be valid for any migrating species where arrival order is of importance.

In this article, we investigate, for different speed and duration variables that determine or reflect the total speed and duration of migration (fig. 1), whether available data from published studies suggest any general tendency of difference between the migration seasons and discuss possible explanations for seasonal differences. More specifically, we test the hypothesis that spring migration is time selected to a higher degree than autumn migration. If this

* Corresponding author; e-mail: cecilia.nilsson@biol.lu.se.

Am. Nat. 2013. Vol. 181, pp. 837–845. © 2013 by The University of Chicago.
0003-0147/2013/18106-5406\$15.00. All rights reserved.
DOI: 10.1086/670335

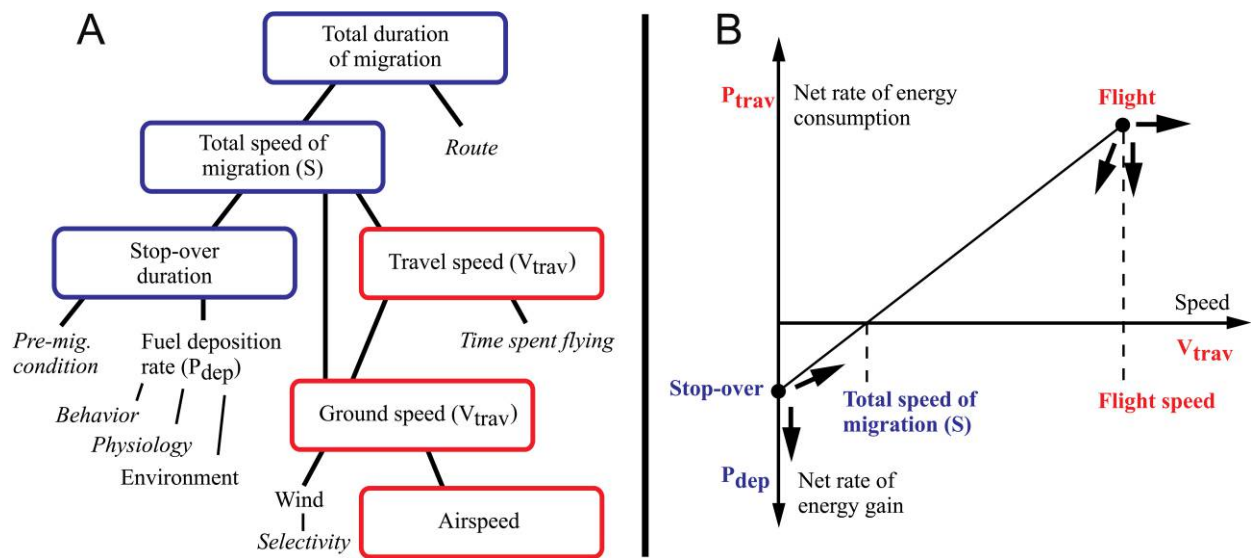


Figure 1: A, Schematic overview of factors that determine total speed and duration of migration. Total duration of migration depends on overall speed of migration and route taken. Total speed of migration depends on duration of stopovers and daily travel speed. Stopover duration depends on premigratory condition and fuel deposition rate, P_{dep} , which in turn depends on foraging rate and efficiency (food abundance, competition, duration of daylight, behavioral and physiological factors; Lindström 1991, 2003). Travel speed is determined by daily travel time and ground speed during traveling. Ground speed, in turn, results from birds' own flight speed in relation to surrounding air (airspeed) and wind conditions. For variables in a box, we evaluated whether seasonal differences occurred. Selection to increase total migration speed (or reduce duration) may operate on behavioral and other traits shown in italics. Variables related to flight behavior are indicated in red, and variables also dependent on foraging behavior are indicated in blue (cf. figs. 1B and 2). B, Total migration speed given graphically in a power-speed diagram as the intercept of the speed axis (X -axis) of the line between energy gain rate on stopover (P_{dep} ; increasing downward) and net rate of energy consumption (P_{trav} ; increasing upward) during flight (V_{trav}). Arrows indicate different ways of increasing total migration speed, for example, by increasing flight speed (tailwind assistance), reducing flight costs (changing flight mode or combining flight with foraging), increasing energy deposition rate, or combining foraging with migratory movement (based on Alerstam 1991, 2011; Hedenström and Alerstam 1998). Variables related to flight behavior are indicated in red, and variables also dependent on foraging behavior are indicated in blue (cf. figs. 1A and 2).

is so, we predict that birds will behave differently during the two seasons, adopting higher flight speeds, larger pre-migratory fuel stores, shorter stopover periods, and increased foraging rates in spring (for more on optimal flight and stopover behavior for time minimization, see Alerstam and Lindström 1990; Alerstam 2011). However, seasonal differences in total speed and duration of migration may be caused not only by different adaptive behaviors between seasons but also by different environmental conditions (e.g., food abundance, wind conditions, length of day/night). Hence, it is perfectly possible that birds behave in an optimal way for minimizing the duration of spring migration but that spring migration is still longer than autumn migration in total duration because of less favorable environmental conditions in spring (e.g., more headwinds, less food). Conversely, spring migration speed may exceed autumn migration speed even if the birds behave in the same way during the two seasons, because of more favorable environmental conditions (e.g., more tailwinds, more food, more daylight for foraging). There-

fore, for each speed and duration variable, we evaluate and discuss whether observed seasonal differences are likely to be caused by differences in adaptive behavior between seasons and/or by different environmental conditions (see fig. 1A). By doing so, we identify what type of observations are needed for distinguishing between behavioral and environmental influences and thus for critically testing the hypothesis of time-selected spring migration. The total speed/duration of migration is determined by both flight speed variables and variables reflecting fuel deposition performance (fig. 1; cf. Alerstam 1991, 2003; Hedenström and Alerstam 1998). The variables determining fuel deposition are expected to have a much stronger impact than flight behavior on the total migration speed (Houston 2000). Thus, we predict that differences between spring and autumn migrations, due to a time-minimizing strategy in spring, will be more pronounced for variables affected by foraging behavior (stopover duration, total migration speed, total migration duration) than for flight speed variables (airspeed, ground speed, daily travel speed). Even

Table 1: Mean, range, and scatter of the ratio between spring and autumn migration speeds/durations for cases in our evaluation, as given by $Q = \log(\text{spring speed/autumn speed})$ or $Q = \log(\text{autumn duration/spring duration})$

Q	Mean	Max	Min	SD	N_{neg}	N_{pos}	N_{tot}	Binomial test (p)
Airspeed	.03	.08	-.03	.04	2	7	9	.09
Ground speed	.04	.23	-.09	.08	4	12	16	.04
Travel speed	.05	.19	-.18	.09	5	13	18	.05
Stopover duration	.23	.89	-1.27	.55	4	23	27	<.001
Total speed of migration	.12	.55	-.35	.21	12	38	50	<.001
Total duration of migration	.10	.56	-.33	.21	16*	36	52	.004

Note: Positive values of Q reflect cases with higher speed (and shorter duration) in spring compared to autumn and vice versa for negative values. Mean, maximum, minimum, and standard deviation (SD) of Q are given for each variable, as well as the number of cases with negative and positive Q values. One-tailed p values were calculated from the number of negative and positive values according to the binomial test (assuming equal probability of negative and positive values). The full data set is available at <http://dx.doi.org/10.5061/dryad.82d4q>.

* Includes one case of $Q = 0$.

though animal tracking studies are rapidly growing in number, the studies available are still too few and often include sample sizes that are too small to allow analyses of seasonal differences in migration between ecological categories of migrants or between age and sex classes. We aim to provide a first general overview of differences in speed and duration between the spring and autumn migrations of all kinds of birds that have been tracked to see whether there are any tendencies toward consistent patterns and to put the findings from tracking studies in the perspective of an ecological and evolutionary framework.

Methods

To avoid the problem of comparing across studies that have used different measures and definitions of migration parameters and that have been based on different tracking methods and sample sizes, we used differences between spring and autumn migrations found within each study included in our analyses. Hence, we included only studies giving information about migration speed or duration for both spring and autumn in our compilation (see <http://dx.doi.org/10.5061/dryad.82d4q>). When a study reported more than one case of migration speed, for example, for two different species or at widely different locations (based on independent samples), each case was included. If a study reported several different speed measurements (e.g., both air- and ground speeds), all variables were included.

Variables considered in this study are airspeed, ground speed, daily travel speed, stopover duration, total migration speed, and total duration of migration. The total migration speed is defined as the total distance (in kilometers) divided by the total duration of migration in days. The daily travel speed is the distance covered on travel days, which is the total duration of migration (days) minus stopover days.

In order to quantify seasonal differences in migration speed and duration, we calculated, for every study and for each available variable, a quotient (ratio). We used the log of the ratio between spring and autumn variables in our evaluation, as given by Q :

$$Q = \log(\text{spring speed/autumn speed}),$$

for speed values

$$Q = \log(\text{autumn duration/spring duration}),$$

for duration values

Positive values of Q reflect cases with higher speed (or shorter duration) in spring compared to autumn (and vice versa for negative values). Furthermore, Q reflects the multiplicative relationship between seasons; for example, a twofold difference in speed (or duration) between seasons will be associated with a $Q = \log(2/1) = 0.30$ (spring speed > autumn speed) or $Q = \log(1/2) = -0.30$ (spring speed < autumn speed), a fourfold difference with $Q = 0.60$ (spring speed > autumn speed) or $Q = -0.60$ (spring speed < autumn speed), and so on. For cases where speed and duration are the same for spring and autumn, $Q = 0$. The Q value should be interpreted with caution, as the studies have very different sample sizes and very different confidences of the estimated values (see, e.g., Chernetsov 2012 for a discussion regarding estimations of stopover time).

Results and Discussion

In a clear majority of cases, spring migration was more rapid than autumn migration (table 1; fig. 2). This was true for all migration variables (fig. 1), but seasonal differences were considerably smaller in magnitude for flight speed variables (airspeed, ground speed, and daily travel speed) than for variables affected by foraging behavior

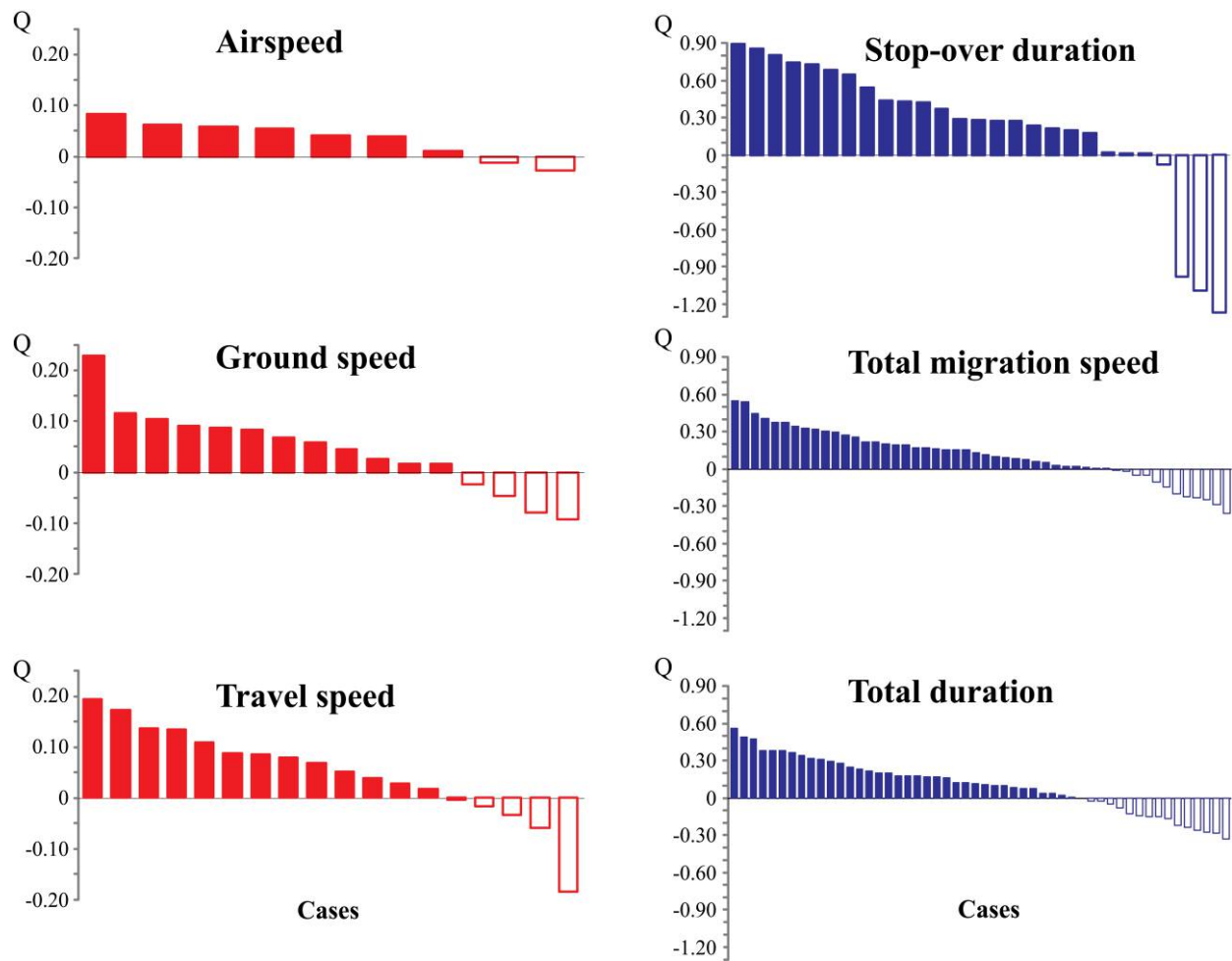


Figure 2: Evaluation of seasonal differences in bird migration performance, in which different variables of migration performance are considered. Variables on the left (red) are related to flight behavior, whereas variables on the right (blue) are also dependent on foraging behavior (cf. fig. 1). Cases are ranked according to the degree of difference in speed/duration. The Q values are the logarithm of the ratio between mean values for spring and autumn, with filled bars indicating cases with higher speed/shorter duration in spring and open bars indicating cases with higher speed/shorter duration in autumn. Individual cases are listed at <http://dx.doi.org/10.5061/dryad.82d4q>. Summary statistics such as mean, minimum, and maximum Q values and sample sizes are given in table 1. Note that the scale on the Y-axis differs between the diagrams on the left- and right-hand sides.

(stopover duration, total migration speed, and total duration of the migratory journey). Nonparametric binomial tests indicated that the predominance of cases with higher speed or shorter duration during spring compared to autumn (the proportion of positive Q values ranged between 69% and 85% for the variables in table 1) was highly unlikely to be caused by random variation for the variables with larger sample sizes. However, the predominance of positive Q values did not reach statistical significance for airspeed, where sample sizes were small (table 1). These tests must, of course, be regarded as highly provisional in light of the differences in samples and accuracy between studies but still provide suggestive evidence in favor of the general hypothesis of time-selected spring migration.

Airspeed

Airspeed (a bird's flight speed relative to the surrounding air) is a unique variable because it is determined solely by the bird's flight behavior (while, in contrast, ground speed is also affected by wind). Airspeed, therefore, constitutes a particularly important attribute for testing the significance of time selection during migration independently of shifting environmental conditions. Paradoxically, changes in airspeed of birds in flapping flight will have only a small effect on resulting migration speed because an increase in airspeed comes at a cost of increased flight power. The optimal airspeed for maximizing total migration speed or minimizing total time of migration is higher than the op-

timal airspeed for minimal energy costs per distance, with an expected difference of 5%–15% (Alerstam and Lindström 1990; Hedenström and Alerstam 1995; Alerstam 2003), leading to an increase in total migration speed of only 0.2%–2% (Houston 2000; Alerstam 2003; Karlsson et al. 2012). Birds are expected to adapt their flapping-flight airspeed not only to different optimization criteria of energy or time minimization but also to flight altitude (air density), wind conditions, and vertical flight speed (climb/descent; Pennycuik 1975; Hedenström and Alerstam 1995).

Seven of the nine cases of airspeed measurements showed positive *Q* values, but absolute *Q* values were small. Two cases regarded passerines, one case swifts, two cases geese, one case shorebird flocks, one case raptors, and two cases all nocturnal migrants at a site (<http://dx.doi.org/10.5061/dryad.82d4q>). The most convincing indication of higher airspeed in spring compared to autumn as an adaptation in time-selected spring migration is from the cases of swifts (Henningsson et al. 2009) and nocturnal long-distance passerine migrants tracked by radar in southern as well as in northernmost Scandinavia (Karlsson et al. 2012). In these cases, most or all of the possible confounding factors (such as seasonal differences in species composition, wind conditions, or body mass) have been taken into account. The consistent findings in these cases, where the difference in magnitude between seasonal airspeeds agreed very well with the expected difference between energy- and time-minimizing airspeeds (Karlsson et al. 2012), provide convincing support of a stronger element of time selection during spring compared to autumn among these migrants. These results stress the need and usefulness of more seasonal comparisons of airspeeds in the future. Especially interesting would be comparisons of airspeeds of specific species, populations, and even individual birds during spring and autumn migrations.

Ground Speed

Ground speeds were, in the majority of cases, also faster in spring than in autumn (table 1; fig. 2), which is in agreement with the hypothesis of time-selected spring migration. However, a seasonal difference in ground speed is in itself much less diagnostic of time-selected behavior than a difference in airspeed. Only in combination with information about airspeed and wind conditions is it possible to critically evaluate whether increased ground speeds are the result of time-selected behavior with respect to selectivity of favorable winds (Thorup et al. 2006; Grönroos et al. 2012).

Cases included passerines, swifts, shorebirds, raptors, and geese, but the number of studies were too few to make comparisons between the groups (<http://dx.doi.org/10>

.5061/dryad.82d4q). Mean *Q* value was similar to that found for airspeed, while the range of *Q* values was larger for ground speed compared to airspeed (table 1; fig. 2). This suggests that the differences in airspeed found between seasons are mirrored in the overall average seasonal difference in ground speed, where the larger range of ground speed *Q* values mainly reflects seasonal differences in wind regimes. Such differences in seasonal wind regimes may explain not only faster ground speeds during spring compared to autumn in some migration systems (e.g., nocturnal migration in the Netherlands; Kemp et al. 2010) but also faster ground speeds during autumn in other systems (e.g., the trans-Saharan migration of Levant sparrow hawks and great snipes; Spaar et al. 1998; Klaassen et al. 2011a).

The possible effects of wind will of course be constrained by the wind conditions available, but within the limits of available conditions, a bird can affect its ground speed by departing on occasions with more favorable winds and by choosing flight altitudes with the most beneficial winds. High ground speeds and a pronounced selectivity for following winds is not necessarily a characteristic of time-selected migration because of the potentially large time costs of waiting for favorable winds to occur. There is an optimal degree of wind selectivity in time-selected migration resulting from the trade-off between the benefits associated with departing on occasions with strong wind assistance and the costs of postponing departure until these occasions occur (Alerstam 1979; Weber et al. 1998; Thorup 2006; Grönroos et al. 2012). The highest degree of wind selectivity would in fact be expected for energy-selected migrants that minimize transport costs for migratory flights. Such migrants are predicted to be very tolerant of long waiting periods and to postpone departure until they can obtain maximal wind assistance that will lead to minimal flight transport costs. Birds can also be selective of wind conditions in evolutionary terms by route choice. In some cases, selectivity of wind regimes may lead to loop migration, where spring and autumn routes differ significantly (Gauthreaux et al. 2005; Shaffer et al. 2006; Klaassen et al. 2011b). We conclude that there is no clear evidence that wind assistance is generally much more important during spring migration. Still, the majority of studies reveal higher ground speeds in spring, which probably is a result of higher airspeeds in spring, possibly in combination with some smaller element of more efficient wind exploitation in spring.

Daily Travel Speed

In 13 of 18 cases in which the distance moved per travel day was calculated, birds covered more distance per travel day in spring than in autumn (table 1; fig. 2). Cases included

mainly passerines, swifts, shorebirds, and raptors, and no obvious differences could be seen between the groups, keeping in mind the small sample sizes within them (<http://dx.doi.org/10.5061/dryad.82d4q>). Birds could achieve longer daily distances by flying at higher ground speeds or by flying for longer periods of the day. An increased daily travel speed is only weakly diagnostic of time-selected behavior. A more detailed analysis of whether longer daily distances are achieved by flying at higher ground speeds or by flying for longer periods of the day (or night) in relation to environmental conditions (wind regimes, length of day/night) is needed. Under some conditions, birds may maximize migration speed by using a fly-and-forage strategy (Strandberg and Alerstam 2007) that will reduce the need for stopovers but at the same time lead to reduced daily travel progress due to foraging activity (Klaassen et al. 2008).

For diurnal migrants, such as raptors using thermal soaring flight, the length of the day can have an influence on flight duration and, hence, travel distance. However, this was not deemed an important factor in a thorough investigation of the daily travel speeds of four raptor species migrating over the Sahara (Mellone et al. 2012). Instead, wind was found to have the biggest impact on daily travel speeds. In addition, after correction for the effect of wind assistance or resistance, there was a pronounced seasonal difference in daily travel speeds across the Sahara desert, with spring speeds exceeding autumn speeds by 20%–40% among two species of long-distance raptor migrants, while short-distance migrants and immature raptors showed similar travel speeds in the two seasons (Mellone et al. 2012). The raptors seemed to achieve their high spring speeds across the Sahara by spending a longer daily period flying and also by using a strategy of mixed soaring and flapping flight. This supports the idea that during spring migration, the long-distance migrants were behaving in a time-selected way, adopting more costly flight behavior to reduce the time for completing their spring migration (Mellone et al. 2012).

Stopover Duration

Seasonal differences in stopover duration (days) were much more pronounced than the differences in air-, ground, and daily travel speeds (fig. 2; table 1). Cases included mainly passerines/swifts, shorebirds, and raptors/storks (<http://dx.doi.org/10.5061/dryad.82d4q>). There are at least four main possible explanations for these pronounced seasonal differences in stopover duration: seasonal differences in (1) feeding conditions (including day length; Bauchinger and Klaassen 2005), (2) degree of premigratory fueling, (3) feeding intensity and feeding behavior, and (4) stopover time not used for fuel deposition.

Many environmental conditions affect feeding condi-

tions (fig. 1B) at a stopover site. Spring migration most often occurs closer to the summer solstice, so days are longer and birds have more daylight to forage during spring than during autumn migration (Bauchinger and Klaassen 2005). This could give the birds the possibility of fattening up faster, leading to fewer stopover days and a higher total speed of migration (Alerstam and Lindström 1990; Kvist and Lindström 2000). In many species of birds, the population of autumn migrants consists to a large part of juveniles born in the same year that may be less efficient foragers compared to adult and experienced birds. This may be the main reason why adults have higher migration speeds than juveniles, according to ringing data for some passerine migrants (Ellegren 1993; but see also Moore et al. 2003 for a case where age did not determine dominance during fuel deposition). During spring migration back to the breeding grounds, all birds have at least some experience, and this might make them more efficient foragers (see, e.g., Jones et al. 2002; Heise and Moore 2003; Gochfeld and Burger 2011).

Birds may often deposit large fuel reserves in their breeding and winter quarters that will help to reduce the need for stopover periods during actual migration. It may be an important strategy for birds to reduce the duration of spring migration by means of extensive premigratory fuel deposition before departure from the winter quarters. Furthermore, birds may have more time for this premigratory fattening in spring than in autumn (when many species may be constrained by breeding requirements and molt, etc.; e.g., Rubolini et al. 2002). The degree of premigratory fueling could also reflect the conditions birds expect to meet during the journey; a high probability of poor fueling conditions will make a high degree of premigratory fueling necessary. More premigratory fattening in spring could also be the result of a selection pressure to exploit the winter quarters for as long as possible and still arrive early at the breeding grounds.

Birds may also reduce stopover duration by feeding more intensively and thus increasing fuel deposition rate. This could, for example, be achieved by adopting a more risk-prone strategy while foraging (Alerstam and Lindström 1990; Lavee et al. 1991). Foraging rate has been shown to be condition dependent (Loria and Moore 1990; Wang and Moore 2005). In time-selected migration, there will be strong selection for efficient and intensive foraging, since the total speed of migration is almost directly proportional to the fuel deposition rate (Houston 2000). Birds may also reduce stopover duration by changing to a strategy of fly-and-forage migration, where foraging is combined with movement in the migratory direction. Even if flight/travel speed will be reduced when movement is combined with foraging, this may be more than compensated for by the reduced need for stopover periods for refueling

(Strandberg and Alerstam 2007; Alerstam 2011; Dias et al. 2012). Nocturnal migrants may achieve particularly high migration speeds by flying during the nights and foraging during the days (without longer stationary stopover periods), as long as the costs of finding and settling at new daily foraging sites and of sleep deprivation are small (Alerstam 2009).

In some cases, birds stop for very long periods (1–2 months) during their autumn migration journeys (e.g., red-backed shrike; Tøttrup et al. 2012). Such a long stop is not likely to be devoted only to fuel deposition for the onward migration journey but may also be considered to represent an additional stationary period (associated with a specific spatiotemporal window of suitable living conditions) in addition to the stationary periods for breeding and for final “wintering” in the annual life cycles of these species (Pearson and Lack 1992; Stach et al. 2012). Including such stationary periods in autumn migration will contribute to exaggerating the difference in migratory performances between the two seasons, although they are still relevant as a contributory explanation for seasonally different patterns of migration.

Studies comparing food abundance and feeding conditions, premigratory fueling, and foraging behavior between the birds’ spring and autumn migrations are necessary for disentangling to what degree the observed seasonal differences in stopover duration are due to behavioral or environmental differences, according to the above explanations.

Total Migration Speed and the Total Duration of Migration

In the majority of cases, birds showed a faster total migration speed and a shorter duration of migration in spring (fig. 2). In cases where the migration routes and thus distances are the same in spring and autumn, Q values for total migration speed and total duration will of course be identical. However, it is becoming increasingly apparent that migration routes may often differ between the two seasons (e.g., for birds completing annual loop migration) and that time minimization in spring may constitute an important selective agent for the evolution of such route differences (fig. 1).

The data set (<http://dx.doi.org/10.5061/dryad.82d4q>) reflects seasonal comparisons of migration speed and duration among five major categories of birds, namely, (1) songbirds, swifts, and hoopoes ($n = 19$ and 14 cases referring to migration speed and duration, respectively), (2) shorebirds, gulls, and terns ($n = 5$ and 7), (3) ducks, geese, and swans ($n = 2$ and 3), (4) oceanic birds (petrels, albatrosses, shearwaters; $n = 2$ and 7), and (5) thermal soaring migrants (raptors, storks; $n = 21$ and 20) and

other migrants ($n = 1$ and 1). Two categories of migrants had enough cases to make comparisons between groups possible: the first, songbirds, swifts, and hoopoes, and the fifth, thermal soaring migrants. There was an overwhelming dominance of cases with shorter duration/higher speed of spring migration in the songbird group, with proportions of positive Q values as high as 93% (total duration, binomial test, $p = .001$) and 89% (total migration speed, binomial test, $p < .001$), respectively. However, for the thermal soaring migrants, there was no clear dominance of a shorter spring duration (50%, binomial test, $p = .6$) and only weak dominance of a faster spring migration (71%, binomial test, $p = .04$). The proportions of positive Q values are significantly different between the songbird and soaring migrant groups for total duration (Fisher exact test, $p = .01$) but not for total migration speed (Fisher exact test, $p = .15$). This may indicate that thermal soaring migrants are not affected by seasonal differences in time selection to the same extent as songbirds and/or that they may be more constrained in changing migration speed because of their special soaring flight behavior. It will be a challenging future task to make more-detailed comparisons between different categories of migrants based on larger data samples to investigate possible fundamental differences in selection pressures or in sensitivity to environmental effects.

The clear dominance of cases where spring migration was more rapid does not mean that the rather few cases where spring migration was slower or more protracted are misleading—in most instances, they probably reflect situations where environmental conditions (seasonal resources and wind regimes) were less favorable during spring compared to autumn migration. However, the clear dominance of cases with faster spring migration strongly suggests there is something more than seasonal differences in environmental conditions that contributes to an explanation of the differences in migration performance; that is, there is a fundamental difference between selective regimes for migration during the two seasons, supporting the idea that time selection is playing a much more important role during spring migration. Interestingly, and in agreement with predictions, seasonal differences were of smaller magnitude for flight speed variables than for variables affected by foraging behavior. It is important to realize that a predominance of cases with faster and shorter spring migration, as demonstrated in this study, can provide only suggestive evidence that birds use a time-minimizing strategy in spring. A fully conclusive test of the time-minimization hypothesis requires that the relative importance of behavioral and environmental factors as explanations for the seasonal differences is clarified, as discussed for the different speed and duration variables above. Studies combining information on the whole mi-

gration with breeding success and survival will be very important for investigating the evolutionary consequences of migration speed and to further testing the time-minimizing strategy.

Concluding Remarks

Our results suggest that comparisons between spring and autumn migrations may serve as a fruitful approach to analyzing migration strategies and evaluating adaptations for minimization of time, energy, and risk in bird migration. It will also be most interesting to compare how the migrations of other taxa differ between seasons and to draw conclusions regarding similarities and differences in selection pressures and environmental conditions.

There has been much debate about whether migratory birds are able to track changes in climate, especially about whether they will be able to arrive earlier in spring to match the advancement of food abundance (Jonzén et al. 2006; Knudsen et al. 2011). Migration speed adjustments could be an important way for migratory birds to adapt to an earlier spring (Both 2010), and there are examples of rate of spring migration being adjusted to environmental factors such as temperature (Marra et al. 2005). If spring migration speed is already close to its limit, however, due to selection for arrival order, the possibility of increasing it even more might be limited. In that case, an earlier departure date from the wintering grounds will be needed, requiring an evolutionary change of the innate response to photoperiod cues that are thought to govern this in many species (Ramenofsky and Cornelius 2012; see also Vardanis et al. 2011; Stanley et al. 2012).

Acknowledgments

We are grateful to J. Bäckman for help with the figures. This work was funded by the Swedish Research Council, and the authors are associated with the Center for Animal Movement Research (CANMove) at Lund University.

Literature Cited

- Alerstam, T. 1979. Wind as selective agent in bird migration. *Ornis Scandinavica* 10:76–93.
- . 1991. Bird flight and optimal migration. *Trends in Ecology and Evolution* 6:210–215.
- . 2003. Bird migration speed. Pages 253–267 in P. Berthold, E. Gwinner, and E. Sonnenschein, eds. *Avian migration*. Springer, Berlin.
- . 2009. Flight by night or day? optimal daily timing of bird migration. *Journal of Theoretical Biology* 258:530–536.
- . 2011. Optimal bird migration revisited. *Journal of Ornithology* 152:S5–S23.
- Alerstam, T., and Å. Lindström. 1990. Optimal bird migration: the relative importance of time, energy and safety. Pages 331–351 in E. Gwinner, ed. *Bird migration: physiology and ecophysiology*. Springer, Berlin.
- Bauchinger, U., and M. Klaassen. 2005. Longer days in spring than in autumn accelerate migration speed of passerine birds. *Journal of Avian Biology* 36:3–5.
- Both, C. 2010. Flexibility of timing of avian migration to climate change masked by environmental constraints en route. *Current Biology* 20:243–248.
- Bridge, E. S., K. Thorup, M. S. Bowlin, P. B. Chilson, R. H. Diehl, R. W. Fléron, P. Hartl, et al. 2011. Technology on the move: recent and forthcoming innovations for tracking migratory birds. *BioScience* 61:689–698.
- Chernetsov, N. 2012. *Passerine migration: stopovers and flight*. Springer, Berlin.
- Dias, M. P., J. P. Granadeiro, and P. Catry. 2012. Do seabirds differ from other migrants in their travel arrangements? on route strategies of Cory's shearwater during its trans-equatorial journey. *PLoS ONE* 7:e49376, doi:10.1371/journal.pone.0049376.
- Ellegren, H. 1993. Speed of migration and migratory flight lengths of passerine birds ringed during autumn migration in Sweden. *Ornis Scandinavica* 24:220–228.
- Fransson, T. 1995. Timing and speed of migration in north and west European populations of *Sylvia* warblers. *Journal of Avian Biology* 26:39–48.
- Gauthreaux, S. A., J. E. Michi, and C. G. Belser. 2005. The temporal and spatial structure of the atmosphere and its influence on bird migration strategies. Pages 182–193 in R. Greenberg and P. P. Marra, eds. *Birds of two worlds*. Johns Hopkins University Press, Baltimore.
- Gochfeld, M., and J. Burger. 2011. Age differences in foraging behavior of the American robin (*Turdus migratorius*). *Behaviour* 88: 227–239.
- Grönroos, J., M. Green, and T. Alerstam. 2012. To fly or not to fly depending on winds: shorebird migration in different seasonal wind regimes. *Animal Behaviour* 83:1449–1457.
- Hedenström, A., and T. Alerstam. 1995. Optimal flight speed of birds. *Philosophical Transactions of the Royal Society B: Biological Sciences* 348:471–487.
- . 1998. How fast can birds migrate? *Journal of Avian Biology* 29:424–432.
- Heise, C. D., and F. R. Moore. 2003. Age-related differences in foraging efficiency, molt, and fat deposition of gray catbirds prior to autumn migration. *Condor* 105:496–504.
- Henningsson, P., H. Karlsson, J. Bäckman, T. Alerstam, and A. Hedenström. 2009. Flight speeds of swifts (*Apus apus*): seasonal differences smaller than expected. *Proceedings of the Royal Society B: Biological Sciences* 276:2395–2401.
- Houston, A. I. 2000. The strength of selection in the context of migration speed. *Proceedings of the Royal Society B: Biological Sciences* 267:2393–2395.
- Jones, J., C. M. Francis, M. Drew, S. Fuller, and M. W. S. Ng. 2002. Age-related differences in body mass and rates of mass gain of passerines during autumn migratory stopover. *Condor* 104:49–58.
- Jonzén, N., A. Lindén, T. Ergon, E. Knudsen, J. O. Vik, D. Rubolini, D. Piacentini, et al. 2006. Rapid advance of spring arrival dates in long-distance migratory birds. *Science* 312:1959–1961.

- Karlsson, H., C. Nilsson, J. Bäckman, and T. Alerstam. 2012. Nocturnal passerine migrants fly faster in spring than in autumn: a test of the time minimization hypothesis. *Animal Behaviour* 83: 87–93.
- Kemp, M. U., J. Shamoun-Baranes, H. Van Gasteren, W. Bouten, and E. Van Loon. 2010. Can wind help explain seasonal differences in avian migration speed? *Journal of Avian Biology* 41:672–677.
- Klaassen, R. H. G., T. Alerstam, P. Carlsson, J. W. Fox, and Å. Lindström. 2011a. Great flights by great snipes: long and fast non-stop migration over benign habitats. *Biology Letters* 7:833–835.
- Klaassen, R. H. G., M. Hake, R. Strandberg, and T. Alerstam. 2011b. Geographical and temporal flexibility in the response to crosswinds by migrating raptors. *Proceedings of the Royal Society B: Biological Sciences* 278:1339–1346.
- Klaassen, R. H. G., R. Strandberg, M. Hake, and T. Alerstam. 2008. Flexibility in daily travel routines causes regional variation in bird migration speed. *Behavioral Ecology and Sociobiology* 62:1427–1432.
- Knudsen, E., A. Lindén, C. Both, N. Jonzén, F. Pulido, N. Saino, W. J. Sutherland, et al. 2011. Challenging claims in the study of migratory birds and climate change. *Biological Reviews of the Cambridge Philosophical Society* 86:928–946.
- Kokko, H. 1999. Competition for early arrival in migratory birds. *Journal of Animal Ecology* 68:940–950.
- Kvist, A., and Å. Lindström. 2000. Maximum daily energy intake: it takes time to lift the metabolic ceiling. *Physiological and Biochemical Zoology* 73:30–36.
- Lavee, D., U. N. Safriel, and I. Meilijson. 1991. For how long do trans-Saharan migrants stop over at an oasis? *Oikos* 22:33–44.
- Lindström, Å. 1991. Maximum fat deposition rates in migrating birds. *Ornis Scandinavica* 22:12–19.
- . 2003. Fuel deposition rates in migrating birds: causes, constraints and consequences. Pages 307–320 in P. Berthold, E. Gwinner, and E. Sonnenschein, eds. *Avian migration*. Springer, Berlin.
- Loria, D. E., and F. R. Moore. 1990. Energy demands of migration on red-eyed vireos, *Vireo olivaceus*. *Behavioral Ecology* 1:24–35.
- Marra, P. P., C. M. Francis, R. S. Mulvihill, and F. R. Moore. 2005. The influence of climate on the timing and rate of spring bird migration. *Oecologia (Berlin)* 142:307–315.
- McNamara, J. M., R. K. Welham, and A. I. Houston. 1998. The timing of migration within the context of an annual routine. *Oikos* 29: 416–423.
- Mellone, U., R. H. G. Klaassen, C. García-Ripollés, R. Limiñana, P. López-López, D. Pavón, R. Strandberg, V. Urios, M. Vardakis, and T. Alerstam. 2012. Interspecific comparison of the performance of soaring migrants in relation to morphology, meteorological conditions and migration strategies. *PLoS ONE* 7:e39833.
- Moore, F. R., S. Mabey, and M. Woodrey. 2003. Priority access to food in migratory birds: age, sex and motivational asymmetries. Pages 281–292 in P. Berthold, E. Gwinner, and E. Sonnenschein, eds. *Avian migration*. Springer, Berlin.
- Moore, F. R., R. Smith, and R. Sandberg. 2005. Stopover ecology of intercontinental migrants: en route problems and consequences for reproductive performance. Pages 251–261 in R. Greenberg and P. Marra, eds. *Birds of two worlds: the ecology and evolution of migration*. Johns Hopkins Press, Baltimore.
- Pearson, D. J., and P. C. Lack. 1992. Migration patterns and habitat use by passerines and near passerine migrant birds in eastern Africa. *Ibis* 134:89–98.
- Pennycuik, C. J. 1975. Mechanics of flight. Pages 1–75 in D. S. Farner and J. R. King, eds. *Avian biology*. Vol. 5. Academic Press, London.
- Ramenofsky, M., and J. M. Cornelius. 2012. Physiological and behavioral responses of migrants to environmental cues. *Journal of Ornithology* 153(suppl.):181–191.
- Robinson, W. D., M. S. Bowlin, I. Bisson, J. Shamoun-Baranes, K. Thorup, R. H. Diehl, T. H. Kunz, S. Mabey, and D. W. Winkler. 2010. Integrating concepts and technologies to advance the study of bird migration. *Frontiers in Ecology and the Environment* 8: 354–361.
- Rubolini, D., A. Massi, and F. Spina. 2002. Replacement of body feathers is associated with low pre-migratory energy stores in a long-distance migratory bird, the barn swallow (*Hirundo rustica*). *Journal of Zoology* 258:441–447.
- Shaffer, S. A., Y. Tremblay, H. Weimerskirch, D. Scott, D. R. Thompson, P. M. Sagar, H. Moller, et al. 2006. Migratory shearwaters integrate oceanic resources across the Pacific Ocean in an endless summer. *Proceedings of the National Academy of Sciences of the USA* 103:12799–12802.
- Spaar, R., H. Stark, and F. Liechti. 1998. Migratory flight strategies of Levant sparrowhawks: time or energy minimization? *Animal Behaviour* 56:1185–1197.
- Stach, R., S. Jakobsson, C. Kullberg, and T. Fransson. 2012. Geolocators reveal three consecutive wintering areas in the thrush nightingale. *Animal Migration* 1:1–7, doi:10.2478/ami-2012-0001.
- Stanley, C. Q., M. MacPherson, K. C. Fraser, E. A. McKinnon, and B. J. M. Stutchbury. 2012. Repeat tracking of individual songbirds reveals consistent migration timing but flexibility in route. *PLoS ONE* 7:e40688, doi:10.1371/journal.pone.0040688.
- Strandberg, R., and T. Alerstam. 2007. The strategy of fly-and-forage migration, illustrated for the osprey (*Pandion haliaetus*). *Behavioral Ecology and Sociobiology* 61:1865–1875.
- Thorup, K., T. Alerstam, M. Hake, and N. Kjellén. 2006. Traveling or stopping of migrating birds in relation to wind: an illustration for the osprey. *Behavioral Ecology* 17:497–502.
- Tøttrup, A. P., R. H. G. Klaassen, R. Strandberg, K. Thorup, M. W. Kristensen, P. S. Jorgensen, J. Fox, V. Afanasyev, C. Rahbek, and T. Alerstam. 2012. The annual cycle of a trans-equatorial Eurasian-African passerine migrant: different spatio-temporal strategies for autumn and spring migration. *Proceedings of the Royal Society B: Biological Sciences* 279:1008–1016.
- van Noordwijk, A. J., R. H. McCleery, and C. M. Perrins. 1995. Selection for the timing of great tit breeding in relation to caterpillar growth and temperature. *Journal of Animal Ecology* 64: 451–458.
- Vardanis, Y., R. H. G. Klaassen, R. Strandberg, and T. Alerstam. 2011. Individuality in bird migration: routes and timing. *Animal Behaviour* 7:502–505.
- Wang, Y., and F. R. Moore. 2005. Long-distance bird migrants adjust their foraging behavior in relation to energy stores. *Acta Zoologica Sinica* 51:12–23.
- Weber, T. P., B. J. Ens, and A. I. Houston. 1998. Optimal avian migration: a dynamic model of fuel stores and site use. *Evolutionary Ecology* 12:377–401.
- Yohannes, E., H. Biebach, G. Nikolaus, and D. J. Pearson. 2009. Migration speeds among eleven species of long-distance migrating passerines across Europe, the desert and eastern Africa. *Journal of Avian Biology* 40:126–134.

Natural History Editor: Mark A. McPeck